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LABORATORY STUDIES OF FEEDING AND MATING IN SPECIES OF *CARCINONEMERTES* (NEMERTEA: HOPLONEMERTEA)

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ABSTRACT

Details of the suctorial feeding behavior of some species of *Carcinonemertes* on crab eggs are described. Under laboratory conditions juvenile and male worms ate an average of 0.6–0.7 crab egg/day. Females ate 2–3 eggs/day. Laboratory feeding rates of worms from different hosts were similar when worms were fed eggs of the same host. No worms ate lobster eggs. Worms grown under laboratory conditions tended to be smaller than similar-aged worms found on hosts. Female worms fed natural host eggs or eggs of unnatural hosts started laying egg strings in a variable number of days. More variability in timing of egg production was observed within a worm species than between species when fed on the same host's eggs. Mating behavior is described for the first time for a species of *Carcinonemertes.*

INTRODUCTION

Along the West Coast of the United States many brachyuran crabs in several families harbor nemerteans of the genus *Carcinonemertes.* These include the grapsids *Hemigrapsus oregonensis, H. nudus,* and *Pachygrapsus crassipes* (Kuris, 1978; Roe, 1979); the cancrids *Cancer magister* (Wickham, 1978), *C. antennarius, C. anthonyi, C. productus* (Kuris, 1978), *C. gracilis* (Stricker and Reed, 1981), *C. jordani* (Roe, pers. obs.); the majid *Pugettia producta* (Coe, 1902; Roe, pers. obs.); and the leucosiid *Randallia ornata* (Roe, pers. obs.). *Carcinonemertes errans* is apparently host specific, being restricted to *Cancer magister* (Wickham, 1978). *Carcinonemertes epialti* was named by Coe (1902) for worms found on *Pugettia producta.* Worms on hosts other than *Cancer magister* are presently considered to be *C. epialti,* although slight differences exist in worms from different hosts (Wickham, 1978). The actual number of species of U. S. west coast carcinonemerteans and degree of host specificity are unknown, especially with respect to the worms called *C. epialti.*

During the crab brooding season, worms on ovigerous females feed, grow to maturity, and lay their own egg strings among the crab eggs (Humes, 1942; Kuris, 1978; Roe 1979; Wickham, 1980). The time required for worms to mature and reproduce is different for crabs with different brooding times, with worm larvae and crab zoeae tending to hatch at the same time. For example, worms on *Hemigrapsus oregonensis* with a brooding period of 44 days in central California, take about 44 days to feed and reproduce and for larvae to hatch (Kuris, 1978; Roe, 1979), whereas in *Cancer magister,* whose brooding season is about 85–90 days in central California, the worm's growth and reproductive period also takes about 85–90 days (Wickham, 1980). During their trophic period worms feed on developing crab embryos and the yolk within the crab eggs.

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Worms on male crabs are thought to be only juveniles since, at least with *Cancer magister,* most worms on male crabs transfer to female crabs at the time of crab mating, whereas none have been observed to transfer from female to male crabs (D. E. Wickham *et al.,* Univ. Calif. Bodega Marine Laboratory, in prep.). Worms on male crabs remain in the juvenile state, apparently being maintained by uptake of dissolved organic materials leaked through arthrodial membrane areas of host crabs (Roe *et al.,* 1981; Crowe *et al.,* 1982). Worms on non-brooding female crabs appear to be juveniles as well, although just after a female releases zoeae, her worms are post reproductive, and shrink. The life span of the worms is still unknown.

Members of all the species of *Carcinonemertes* used in this study exhibit sexual dimorphism. Females become larger than males and have a bluntly pointed posterior end. In addition, the gut diverticula appear more pronounced in females. Males are smaller, appear to have fewer and less regularly arranged gut diverticula, and the posterior end is truncate to concave. At maturity gametes also show through the body wall; the previously mentioned features appear before worms are fully mature.

Carcinonemertes errans exists in epidemic numbers on the commercially important dungeness crab, *Cancer magister,* in central California, Oregon, and Washington (Wickham, 1979), and because the worm eats crab eggs and exists in such large numbers, it has been implicated in the collapse of the central California dungeness crab fishery (Wickham, 1979). Efforts are being undertaken to understand the relationship between worms, host, and fishery and to control worms on *Cancer magister* (Kuris, 1981–1982). Mortality of crab eggs due to feeding by *C. errans* in nature has been estimated to be about 70 eggs/worm brooding season (Wickham, 1979), and Hamilton (1984) found similar feeding rates by *C. errans* under laboratory conditions.

This study was designed to (1) describe feeding behavior, (2) determine the basic feeding rates of worms from *Hemigrapsus oregonensis* on *H. oregonensis* eggs, (3) determine host egg specificity in feeding by *Carcinonemertes errans* and by worms on other available hosts, and (4) compare feeding between worms from different hosts. Results should provide information on some aspects of host specificity and on complexity of possible control measures for *C. errans.*

MATERIALS AND METHODS

Hemigrapsus oregonensis was picked from under intertidal rocks at Bodega Harbor and Elkhorn Slough; *Cancer magister,* two males of *C. antennarius,* and one male *Randallia ornata* were collected in crab traps by commercial fishermen near Bodega Bay, and one brooding female of *Cancer jordani* was collected from a sea water intake screen at Bodega Marine Laboratory. Crabs were held in sea water tables at Bodega Marine Laboratory (12–14°C) or in aquaria in a constant temperature room at California State College Stanislaus (about 12°C).

Worms and crab eggs were removed from crabs by fine forceps and worms were held either individually or in groups with a small cluster of crab eggs. Most worms and eggs were kept in covered 5-cm disposable plastic petri dishes, although a few were held in one of the two different designs of flow-through worm holders designed by Hamilton (1984) and R. Okazaki (Bodega Marine Laboratory and U.C., Santa Barbara). The flow-through containers had the advantage of constant water exchange, but worms sometimes escaped. The petri dishes were large compared to the size of worms and clump of eggs each contained, and appeared to provide an adequate environment for the worms. Since the petri dish containers were easier to work with, they were used in most experiments. Sea water in petri dishes was changed occasionally. Containers with worms were kept on the sea water tables in Bodega Marine Laboratory or in the constant temperature room at California State College Stanislaus. For quantitative feeding experiments the number of healthy crab eggs added to a container with a worm was recorded. After a time lapse of a few days, the number of partly or completely eaten eggs was recorded. Uneaten eggs or fresh eggs were then left in the container with the worm. When eggs are completely eaten only the egg membrane is left; when eggs are partly eaten a string of yolk is seen coming out of the egg, the contents inside are reduced, or there is a large clear space inside. Since the crab embryo is killed even if only partly eaten, and since, for most of the worm feeding period, nearly the entire contents of eggs are eaten, partly eaten eggs are considered eaten in this study. The terms egg or crab egg refers to fertilized, extruded eggs developing into embryos during the crab brooding period.

Many experiments were set up to see whether worms from one host would eat and develop if given eggs from another host. In these situations small clusters of eggs were added to containers with one or more worms as before, but were not counted. Time from feeding until the first worm egg string was produced was recorded for these experiments.

The following combinations of worms and eggs were made: worms from *Hemigrapsus oregonensis* with eggs from *H. oregonensis, Cancer jordani, Cancer magister,* and the lobster *Homarus americanus;* worms from *Cancer magister* with eggs from *C. jordani, H. oregonensis,* and *H. americanus;* one female and one male worm from *C. jordani* with eggs from *C. jordani* and *H. oregonensis;* worms from *Cancer antennarius* with *H. oregonensis* eggs; and one worm from *Randalli ornata* with *H. oregonensis* eggs. Since ovigerous females of *Hemigrapsus oregonensis* can be easily collected during any good low tide, their eggs were the most readily available and were the ones most frequently used in the experiments.

Some worms (25–50% of the total) in nearly all experiments would not feed, on natural or unnatural host eggs. For this reason, many worms were sometimes put in with a cluster of crab eggs for a few days before start of an experiment. Only worms that fed during the initial period were used in the experiment. Also, feeding rates were calculated only from worms that did eat.

Except for *C. errans,* worms were usually identified by their natural host rather than by species, since the actual number of species, and host specificity, is unknown for the group called *Carcinonemertes epialti.*

RESULTS

Description of feeding behavior

The feeding behavior of species of *Carcinonemertes* when eating crab eggs is typical of suctorial feeding among nemerteans as described by McDermott (1976). A worm spreads its anterior end against a crab egg (see picture in Wickham, 1978), apparently makes a hole in the egg membrane with its stylet, then inserts its foregut into the egg (Wickham, 1979; Roe, pers. obs.). The proboscis of *Carcinonemertes* apparently does not secrete toxin: on one occasion, when a worm was feeding on old embryos, the embryo that was being fed upon was much more active than other embryos in the egg cluster.

The foregut is muscular; one can observe it to undergo peristalsis, to move around within the egg, and to be more and less everted often while it is within the egg. A rather strong suction is apparently created by the foregut: I have seen the pigment comprising the eye of a developing zoea being pulled out of the circular eye into an elongate stream of pigment particles flowing into the gut. In addition, yolk is sometimes pulled out of the egg beyond the egg membrane. The ciliated stomach is probably also important in drawing food into the worm.

Particles of yolk and more fluid parts of developing zoeae flow into the foregut and on into the worm. Since the yolk of *Hemigrapsus oregonensis* eggs is dark brown, it can easily be seen streaming into the gut through the thin, orange nemertean body wall. The gut fills from the posterior end, and the worm diameter increases as the gut fills. The gut can be filled to just posterior of the position of the middle chamber of the inverted proboscis, but worms sometimes quit feeding before the gut is completely filled.

Small worms tend to flatten their anterior end against an egg more than larger worms; the head of larger worms is often only barely wider than the body while the worm is feeding. The anterior end of the body can undergo peristalsis along with the foregut, or the worm can lie still during feeding. A worm can also lose contact several times with the prey egg before it is finished feeding. I have seen worms pull away from their food, then return to it immediately up to 7–8 times during a single feeding episode.

In feeding observations of three juveniles and one female it took approximately 30 minutes, from soon after feeding commenced until finished, when the worm pulled away from the egg, turned, and crawled away. Often a stream of yolk is left protruding from a partially eaten egg, especially if eggs are young (recently extruded, with much yolk material). Once, a second worm was observed to feed on protruding yolk made by another worm, before the first one was finished eating. Multiple use of crab eggs might be a partial explanation for the apparent depression in feeding rate with increased worm density observed by Wickham (1979).

Feeding by worms from Hemigrapsus oregonensis *on eggs of their natural host,* H. oregonensis

Data for laboratory feeding rates and duration of different life history stages of worms for worms taken from *Hemigrapsus oregonensis* are summarized in Table I. Individual worms (followed through development) that grew into males showed an increased feeding rate as they became mature; it took about 20 days before they had developed enough to be recognized as males. Males tended to eat in the first few days

TABLE I

Laboratory feeding rates of worms from Hemigrapsus oregonensis *on eggs of* H. oregonensis

Worm life stage	Average feeding rate (eggs/day ± 1 S.D.)	Number of worms in sample	Duration of life stage (days ± 1 S.D.)
JUVENILE			
overall	0.63 ± 0.26	16	—
juvenile to male	0.69 ± 0.22	5[1]	19.8 ± 4.49
juvenile to female	0.92 ± 0.25	3[2]	16.0 ± 3.50
MALE			
overall	0.74 ± 0.67	9	—
mature	1.3 ± 0.58	4[1]	14.3 ± 7.18
post-reproductive	0.2 ± 0.14	4[1]	19.3 ± 4.92
FEMALE			
overall	2.14 ± 0.71	10	—
mature	2.4 ± 1.0	3[2]	17.3 ± 1.53
post-reproductive	0.14 ± 0.10	4	11.8 ± 2.87

[1,2] Same individuals through time. Number of worms in sample is the same for Average feeding rate and Duration of life stage in each category.

after they could be recognized as males; after they reached assumed maturity, feeding dropped to almost nothing (see mature and post-reproductive males, Table I). Older males would move away from the eggs and become quiescent, usually at the edge of the container.

Juvenile worms that grew into females had a higher feeding rate as juveniles than those that developed into males (Table I), and it only took about 16 days from the start of experiments to recognize them as immature females. The trophic period of females was longer than that of males (Table I), and females consumed eggs at the greatest rate (and actual number) of any of the life history groups.

The feeding rate for all actively metabolizing, egg producing females (Table I, overall female category) included several worms that had matured on host crabs before experiments were started, so the duration of active feeding and egg laying was not determined for this group (Table I). However, as with males, after the reproductive period was over, females reduced their feeding rate considerably. In addition, of 8 post-reproductive females removed from crab hosts to see if they would feed on recently extruded crab eggs or crab eggs about to hatch, 7 did not feed for at least 16 days and 1 worm ate 11 young eggs in 25 days (=0.44 egg/day for that worm).

The first egg strings produced by the three females followed throughout their development (Table I) appeared about 31 days (Table II) after feeding started, and these females grown from juveniles in the laboratory laid an average of 5.6 (S.D. = 5.03) egg strings. Their reproductive output can be compared to an average of 6.4 (n = 5, S.D. = 1.140) egg strings laid by females taken from hosts after they had already developed into females. Experimental females tended to be smaller than females taken from hosts (average length of 3 females grown from juveniles = 4.67 mm, S.D. = 1.258; average length of mature females collected from host for feeding experiments = 6.5 mm; average length of 47 females of varying degree of maturity from host crab = 5.18 mm, S.D. = 1.59). Experimental males were also smaller than males from nature, (laboratory reared, average = 1.97 mm, S.D. = 0.43, n = 7; males from host crabs, average = 2.81 mm length, S.D. = 0.544, n = 43).

TABLE II

Average number of days ± 1 S.D. from start of experiment to production of first worm egg string, by worms fed eggs of various hosts

	Egg Species		
Worms from host crabs	*Hemigrapsus oregonensis*	*Cancer magister*	*Cancer jordani*
Hemigrapsus oregonensis	31 ± 1.00 (3)	16 or 29 (1)	14 (1)
Cancer magister	F-36.2 ± 9.43[1] (6)		
	W-42.0 ± 5.07[1] (8)		
	S-28.7 ± 3.86[1,2] (7)		
	O-36.4 ± 8.46 (21)	—	19 (1)
Cancer antennarius	23.2 ± 1.66[2] (11)	—	—
Randallia ornata	21 (1)	—	—

Numbers in parentheses are the numbers of worms in the samples; F = fall, W = winter, S = summer, O = overall.

[1] Difference between median number of days to reproduction fall/winter *versus* summer significant at 0.2 level, Mann-Whitney U Test.

[2] No significant difference between median number of days to reproduction in summer for worms from *C. magister versus C. antennarius*, 90% level, Mann-Whitney U Test.

From feeding rates and days of feeding, it was calculated that a typical worm developing into a female would consume approximately 57 eggs in 45 days and a typical worm growing into a male would eat 36 eggs in 53 days. Using only the subsample of two worms that actually grew from juveniles into adult, then post-reproductive males, the total egg consumption of males was 22 eggs in 34 days.

Feeding on eggs of Hemigrapsus oregonensis *by worms found on other hosts*

Individuals of *Carcinonemertes errans* were the most studied with respect to feeding rate, since *C. errans* is a known different species from worms on other hosts. Data for laboratory feeding rates and duration of various life history stages of *C. errans* eating eggs of *Hemigrapsus oregonensis* are summarized in Table III.

Those juveniles that developed into males had a somewhat lower feeding rate than the average juvenile (Table III). As they developed into adults, the feeding rate increased. It took longer for these animals to mature than it took worms from *H. oregonensis* (Table I), but they remained active feeding adults for about two weeks, as did the males from *H. oregonensis* (Table I). Post-reproductive worms quit eating (Table III). Juveniles that developed into females had a higher feeding rate than the other juveniles, and mature females had the highest feeding rate of all life history categories (Table III). Again, it took longer to recognize these animals as immature females than it did with worms from *H. oregonensis,* but they remained adults approximately the same amount of time (Tables I, III). In the four animals followed from juvenile through female stage, after they were recognizable as females but before they were sexually mature, the worms ate more than they did as juveniles but less than they did as mature females (see immature and mature female stages, Table III). Eleven females laid an average of 5.4 egg strings (S.D. = 0.75) and reproduction started about 36 days after feeding commenced (Table II).

Time to first reproduction varied considerably between test groups of *C. errans* (Table II). The difference between the median time before first reproduction in fall-winter *versus* summer was significantly different at the 0.2 level using the Mann-Whitney U Test. By contrast, the difference between the median time of first repro-

TABLE III

Laboratory feeding rates of Carcinonemertes errans *on eggs of* Hemigrapsus oregonensis

Worm life stage	Average feeding rate (eggs/day ± 1 S.D.)	Duration of life stage (days ± 1 S.D.)
JUVENILE		
overall	0.65 ± 0.30 (10)	—
juvenile to male	0.33 ± 0 (2)	24.8 ± 3.36 (28)
juvenile to female	0.84 ± 0.25 (5[1])	25.7 ± 4.24 (23)
MALE		
mature	0.66 ± 0.28 (4)	12 ± 2 (3)
post-reproductive	0 ± 0 (4)	4 (4)
FEMALE		
overall mature	3.2 ± 1.77 (6)	14.2 ± 5.42 (6)
immature	2.46 ± 1.83 (4[1])	8.3 ± 2.06 (4[1])
mature	3.5 ± 1.89 (4[1])	12.25 ± 2.06 (4[1])
post-reproductive	0.26 ± 0.23 (3)	7 ± 1.73 (3)

[1] Same individuals through time. Numbers in parentheses are the numbers of worms in the samples.

duction of summer-grown worms from *Cancer magister* and worms from *C. antennarius* was not significant (90% level, Mann-Whitney U Test, Table II, and section on feeding on alternate host eggs and reproduction, below).

After reproduction, females reduced feeding (Table III) before experiments were terminated. Experimental females grew to an average of 5.83 mm length (n = 6, S.D. = .97); experimental males to 2.6 mm (n = 4, S.D. = 0.35).

Using above figures the calculated egg consumption of a typical *C. errans* female through her life cycle is about 68 eggs in 48 days. Typical egg consumption of a male is about 16 eggs in 37 days.

Results of Mann-Whitney U Tests comparing median feeding rates of worms from *H. oregonensis* on natural host (*H. oregonensis*) eggs and of *Carcinonemertes errans* on *H. oregonensis* eggs showed no significant differences between the following pairs: juvenile, male, or mature female feeding rates (Table I, III; U statistic, two-tailed test, 90% significance level).

The one brooding female of *Cancer jordani* that was available harbored only a few worms, which were already mature at the time of collection. The one mature female worm tested ate an average of 3.4 *C. jordani* (natural host) eggs/day for five days. During this time she laid three egg strings. The same female was then presented with *H. oregonensis* eggs (and none from *C. jordani*); during the next seven days she ate an average of 3.1 *H. oregonensis* eggs/day and laid three more egg strings. After that she quit eating, even when presented with *C. jordani* eggs. Her feeding rate on *H. oregonensis* eggs was similar to that of worms from other hosts (Tables I, III), and her feeding rate was similar on her own host and on *H. oregonensis* eggs. Her size (7.2 mm) and six egg strings were also similar to other worms. In addition, the experiments with the *C. jordani* female indicate that imprinting on one species of host egg does not occur.

A male worm from the *C. jordani* ate 0.25 egg/day of *H. oregonensis* eggs for eight days. This animal was was thought to be a post-reproductive male since males appear to mature sooner than females, since the female from the same host was already mature, and since the crab's zoeae hatched within 18 days of the start of this experiment. Again, the feeding rate is similar to that of other post-reproductive male worms (Tables I, III).

One juvenile worm was found on a male *Randallia ornata.* It had a juvenile feeding rate of 0.79 *H. oregonensis* eggs per day, grew into a female, and laid one egg string within 21 days after feeding started.

Feeding on alternate host eggs and reproduction

In addition to eating eggs of their natural host, worms from *Hemigrapsus oregonensis* fed, grew, and reproduced on eggs of *Cancer magister* and *C. jordani.* About eight juvenile worms placed with a clump of *C. jordani* eggs became pale when feeding on the golden yolk of these eggs. Worms started making egg strings in 14 days. Of the worms in this experiment, two grew into males, 3 mm and 1.5 mm in length, and two grew into females, 3.5 mm and 5.5 mm in length.

About eight juveniles put with a cluster of *Cancer magister* eggs fed, grew, and reproduced on these eggs also. The eggs became fouled with fungus, bacteria, and ciliates soon after the experiment started, and worms did not appear to be feeding successfully on the fouled eggs. They remained small, although several of them could usually be found on the eggs rather than on the sides or bottom of the fingerbowl. The experiment was re-started with 4 of the original juveniles and fresh *C. magister* eggs after 13 days. Within six days after the fresh crab eggs were added the worms were considerably larger and their guts were orange from the orange-colored egg yolk; within 10 days sexes could be determined (2 young females, 3.5 mm and over 2.5 mm, and 1 male, 1.5 mm). On the 10th day, between the time of removal of crab eggs and replenishment with fresh eggs (about 5 mins.), I realized the male was mating with the smaller female. Mating has never before been described for any species of *Carcinonemertes.* The worms became arranged with their posterior ends together. The male (especially the posterior part of the worm) underwent peristalsis to move backwards to touch the female. The front end of the male only moved if he lost contact with the female; in fact, his head anterior to his eyes seemed compressed and flattened (to gain traction?) on the dish bottom. The female was quiescent but did crawl forward (away from the male) a bit, then would back towards him again. The male would place his posterior end over a small area of the female. The posterior truncate-to-concave end of the male was quite active, and appeared to form a firmly attached muscular cup over each area contacted on the female. As the female backed up to the male, his posterior end appeared to service each gonopore along the female's side. Worm egg strings were produced 6 days later (16 days after the experiment was re-started with clean eggs or 29 days after the start of the experiment, Table II). Mature females were 3.5 and 5 mm long; the male remained 1.5 mm long.

Seven reproducing females from a female *H. oregonensis* were placed in a fingerbowl with recently extruded eggs of the American lobster, *Homarus americanus.* Although worms were sometimes found on these eggs, and although they continued to lay egg strings, none fed on the lobster eggs. Three individuals even seemed repelled by yolk from a broken egg, backing away then turning and crawling off after contact with the yolk.

In addition to *H. oregonensis* eggs, *Carcinonemertes errans* fed, grew, and reproduced on *C. jordani* eggs. Approximately 12 juveniles of *C. errans* ate and became pale from the light-golden yolk of *C. jordani* eggs. The first egg string was produced in 19 days (Table II). *C. errans* was not tested with eggs of its normal host, *C. magister,* because this had already been done (Hamilton, 1984).

Juveniles of *C. errans* placed with recently extruded eggs of *Homarus americanus* did not feed on the lobster eggs in seven days. Some juveniles were found among the eggs, but most were observed to be on the bottom or sides of the fingerbowl, away from the eggs.

Juveniles from *Cancer antennarius* placed with eggs of *Hemigrapsus oregonensis* produced an average of 5.3 (S.D. = 0.82, n = 6 females) egg strings in an average of 23.2 days (Table II).

Importance of age of crab eggs

Attempts made to determine if age of crab eggs was important with respect to feeding rate did not provide clear results. Worms seemed to eat primarily yolk (food reserves), which became only a small portion of the crab eggs as embryos approached hatching. It is possible, although not proven by this study, that decreasing yolk in normal host eggs is the cue that initiates decreased feeding and worm shrinkage after worm reproduction. Several examples suggest the above: a male from *H. oregonensis* ate 18 eggs in 23 days, then 0 near-hatching eggs in the next 8 days, but ate 4 younger eggs in the next 11 days. A female from *H. oregonensis* ate 32 eggs in 17 days, then 2 near-hatching eggs in 14 days, then 12 younger eggs in the next 11 days. In an experiment with four post-reproductive females with near-hatching eggs and four mature-to-post-reproductive females with young crab eggs, the only animal to eat was a post-reproductive female provided young eggs (11 eggs in 25 days). However, some *C. errans* individuals did eat near-hatching eggs of *H. oregonensis* when those were the only food provided. Some of the differences in how long it took developing females to commence egg laying (Table II, especially for worms from *C. magister*) might be explained by noting that animals in fall and winter were fed different-aged eggs from several female crabs. On the other hand, individuals of *C. errans* in summer and worms from *Cancer antennarius* (Table II) were fed eggs from the same females of *H. oregonensis;* the eggs these worms ate were therefore the same age. Finally, in monitoring the development of worms on a female of *C. magister* that died before her zoeae were released, I found that when development of the crab eggs became arrested prior to the crab's death, reproductive development of her resident worms also ceased.

Egg preference of worms from Hemigrapsus oregonensis *and* Cancer magister

In the few attempts made to determine host egg preference, by putting worms from either *Hemigrapsus oregonensis* or *Cancer magister* into a container with clumps of eggs from both crab species, results showed no strong preference of worms for their own host eggs. Worms were found on, and ate, both types of eggs.

Importance of egg contamination

On several occasions crab eggs used in the experiments became fouled with what appeared to be filamentous fungi. The typical behavior of worms with fouled eggs was to decrease or stop feeding, and crawl as far from the egg clump as possible. In a few cases, worms from *H. oregonensis* actually died in such conditions. When fouled eggs were exchanged for healthy ones, worms would usually return to feeding. However, the hiatus in feeding due to fouling may be a major cause for some of the variations in time to first reproduction. Examples include worms from *H. oregonensis* on eggs of *C. magister* (Table II), the difference in fall-winter and summer time to reproduction for *Carcinonemertes errans* (Table II), and at least one experiment during fall with *C. errans* on *H. oregonensis* eggs. Some of the low feeding rates may also reflect problems with egg fouling.

Discussion

These studies indicate that species of *Carcinonemertes* from various hosts will readily feed, grow, and reproduce on their own or alternate crab host eggs. The feeding rates of worms from different hosts were basically similar, when these worms were fed the same species of crab eggs. Likewise, in experiments in which worms were fed eggs of various hosts, the time for worms to mature and lay their first egg strings was more variable within worm species than between worms from different hosts, when both were fed on the same species of eggs. Much greater differences in feeding rate occurred between juveniles and males *versus* females than between worms from different hosts; and the worms from different hosts would probably have even more similar feeding rates and times before the first egg strings were laid if experiments were controlled more carefully with respect to crab egg contamination and age of crab eggs used as food. The worms from different hosts appear to have similar requirements and appear to be quite uniform with respect to basic feeding and developmental rates when they are away from normal host influences. These same worms display markedly different timing in development and egg laying when on their normal hosts. The examples of a 44-day period of feeding, development, and release of larvae in worms on *Hemigrapsus oregonensis* (Kuris, 1978; Roe, 1979) *versus* an 85–90 day period for the same events in *Carcinonemertes errans* on central California *Cancer* *magister* (Wickham, 1980) coupled with the present laboratory situations for both these worms, indicate that many of the differences between worms from different hosts are responses to crab environment rather than intrinsic differences in the worms.

Since worms from several hosts had such similar feeding and reproductive rates in these experiments, these rates can probably safely be used as typical for the carcinonemerteans on most brachyuran hosts, at least along the California coast, under laboratory conditions. Hamilton (1984) found similar laboratory feeding rates for *C. errans* on eggs of its normal host, *C. magister.* In addition, these laboratory feeding rates, especially for female worms, are comparable to estimates made by Wickham (1979) of *C. errans* feeding rates in nature. He estimated that individual worms eat an average of 70 eggs during a brooding period of *C. magister.* In these laboratory feeding experiments females of worms from *H. oregonensis* were estimated to eat about 57 eggs, and females of *C. errans* to eat about 68 eggs as they completed their reproductive cycles.

Although worms from various hosts readily ate eggs of other brachyuran species, neither worms from *H. oregonensis* nor *Carcinonemertes errans* attempted to feed on lobster eggs. Lobster eggs may not be attractive to the worms, or they may simply be too large or have too thick or tough membranes for the worms to handle. The eggs of the three species of crabs used were of similar size, eggs of *H. oregonensis* and *C. jordani* being about 0.3–0.35 mm and eggs of *C. magister* being about 0.42 mm in diameter. Lobster eggs were much larger (about 1.7–1.8 mm diameter) than the brachyuran eggs. Fleming and Gibson (1981) recently described *Pseudocarcinonemertes homari* found on the American lobster and thought to eat lobster eggs. *P. homari* has a stylet about twice as long (average 21.2 μm, Fleming and Gibson, 1981) as the stylets of West Coast *Carcinonemertes* used in this study (10.3–11 μm, Wickham, 1978). In addition, the proboscis of *P. homari* is eversible beyond the front end of the worm and is a rather substantial structure, in contrast to the small proboscis of *Carcinonemertes.* Membranes of lobster eggs show thick and thin areas. Thick parts are about 7.5 μm wide, and thinner areas are about 3.8 μm wide, so the stylets of *Carcinonemertes* from brachyuran crabs are longer than the thickness of lobster egg membranes and should be able to penetrate the membranes. However, it is not known whether the *Carcinonemertes* proboscis has the power to effect penetration. Possibly, the worms normally found on brachyuran hosts cannot penetrate the thick, tough lobster egg membrane.

These studies indicate a low level of host specificity in feeding biology of West Coast species of *Carcinonemertes.* Worms from *Cancer magister* and *Hemigrapsus oregonensis* placed into a fingerbowl will also crawl onto and remain on unnatural hosts (Roe, unpubl.). Nothing is known about host selectivity by settling worm larvae, and worms may show much host specificity at that point in their life history. However, if worms do find themselves on unusual hosts, or if host specificity is actually low, they can certainly complete their life history on a variety of hosts.

Carcinonemertes errans occurs in epidemic numbers on *Cancer magister* (Wickham, 1979) and efforts are underway to find methods to control numbers of this worm on this commercially valuable host (Kuris, 1981–1982). If these worms show little host specificity, or if even a small portion find themselves on alternate sympatric hosts, then results from this study would indicate that effective control of the worms will be more complex than previously thought. Similar rationale pertains to the *Carcinonemertes epialti* group found on several potentially commercially valuable species.

These studies also broadened the potential for several types of laboratory studies of *Carcinonemertes.* One or another species of brachyuran crab with ovigerous females can usually be found along the U. S. west coast any time, and since the worms successfully eat a variety of eggs, several types of experiments will no longer be confined to the sometimes highly seasonal normal host brooding period. In addition, if several "species" of worms are fed on eggs of the same crab host, sources of variability between worms due to food can be eliminated. Such information will be useful in electrophoretic studies of worms as part of determination of the actual number of worm species found on the U. S. west coast (D. E. Wickham, U. C. Davis and Bodega Marine Laboratory, pers. comm.).

A totally unexpected result from these experiments was the observation that worms taken from male crabs and presumed to be sexually immature, and raised in isolation, laid egg strings in which the eggs developed anyway (Roe, pers. obs.). Although the mechanism of producing larvae by single individuals was not determined for the present study, the result nevertheless adds more complexity to the study of the number of worm species. The idea of putting male worms from one host with females of another host to see if they produce viable offspring is a naive, unworkable method to determine species of west coast *Carcinonemertes.*

This research opens avenues of study previously unrecognized as useful, and at the same time, indicates that some problems with respect to the west coast species of *Carcinonemertes* are more complex than previously thought.

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